

TAXONOMY OF THE MOST COMMON WEEDY EUROPEAN
ECHINOCHLOA SPECIES (POACEAE: PANICOIDEAE)
WITH SPECIAL EMPHASIS ON
CHARACTERS OF THE LEMMA AND CARYOPSIS

Mihai Costea¹

Department of Plant Agriculture
University of Guelph
Guelph, Ontario, N1G 2W1, CANADA
coste_amihai@hotmail.com

François J. Tardif

Department of Plant Agriculture
University of Guelph
Guelph, Ontario, N1G 2W1, CANADA
ftardif@uoguelph.ca

ABSTRACT

The most common weedy *Echinochloa* species in Europe—*E. colona* (L.) Link, *E. crus-galli* (L.) Beauv., *E. hispidula* (Retz.) Nees ex Royle, *E. oryzoides* (Arduino) Fritsch, *E. oryzicola* (Vasing.) Vasing. are for the first time analyzed regarding the micromorphology of lemma and caryopsis, the anatomy of the caryopsis and the size of the starch grains. New potentially valuable characters are the size of the caryopsis, the pattern of surface variation of the caryopsis coat, and the size of the starch grains. A cautionary approach is suggested towards the taxonomic utility of the silica bodies shape. Based on the new characters, the relationships between the species are analyzed. Some nomenclatural issues involving *E. oryzicola*, *E. oryzoides*, and *E. hispidula* are also discussed. For the first time, *E. colona* is recorded from Romania.

RESUMEN

Las especies más comunes de *Echinochloa* en Europa que son *E. colona* (L.) Link, *E. crus-galli* (L.) Beauv., *E. hispidula* (Retz.) Nees ex Royle, *E. oryzoides* (Arduino), Fritsch, *E. oryzicola* (Vasing.) Vasing. han sido analizadas por primera vez mediante micromorfología del lemma y del cariósipide, la anatomía del cariósipide y por el tamaño de los granos de almidón. Los nuevos caracteres que se pueden considerar de gran valor son el tamaño del cariósipide, la variación en el patrón de la superficie de la cubierta del cariósipide y el tamaño de los granos de almidón. No se sugiere como herramienta taxonómica la forma de los cuerpos silíceos. Basándose en los nuevos caracteres, se analiza la relación entre las especies. Algunos tópicos de nomenclatura que involucran a *E. oryzicola*, *E. oryzoides* y *E. hispidula* son también discutidos. Por primera vez *E. colona* se cita de Rumania.

INTRODUCTION

Echinochloa is an economically important genus because many of its species are noxious weeds. In Europe, *E. hispidula*, *E. oryzoides* and *E. oryzicola* are most often found as weeds in rice fields while *E. crus-galli* and *E. colona* although present in rice fields, are more often encountered in irrigated fields and amongst vegetable crops (Kossenko 1947; Vasconcellos 1954; Pirola 1965; Chirilă 1984; Tzvelev 1976; Häflinger & Scholz 1980; Carretero 1981; Mosyakin 1996; Ciocarlan 2000). The taxonomy of the genus is controversial due to nomenclatural prob-

¹Corresponding author

lems and the continuous morphological variation exhibited by the taxa. For the practical purpose of plant identification, the species often lack conspicuous identification characters. Previous treatments and taxonomic studies are often contradictory and, consequently, the limits of the taxa are uncertain and specimens in herbaria are often misidentified. Other important taxonomic treatments of the genus (or part of the genus) are those of Stapf (1899, 1934), Hitchcock (1920), Wiegand (1921), Kossenko (1947), Ohwi (1942, 1962), Martinez Crovetto (1942), Vasconcellos (1954), Bor (1960), Pirola (1965), Chirilă (1967, 1984), Yabuno (1962, 1981), Ali (1968), Gould et al. (1972), Tzvelev (1976), Häflinger & Scholz (1980), Clayton (1980), Carretero (1981), Michael (1983) and Brussoni (1994). A general characterization of the genus can be found in Watson and Dallwitz (1992–onwards). Carretero (1981) provided a summary of the morphologic characters for European weedy species of the genus *Echinochloa*.

The identification of new characters useful in determining taxonomic boundaries have shed light on our understanding of difficult groups such as grasses. The study of lemma micromorphology can provide characters valuable in elucidating the delimitation of taxa, and these characters may reflect systematic relationships. Micromorphological features of glumes and bracts (lemma and palea) have been studied in other genera from *Poaceae* by: Bjorkman (1960), Hsu (1965), Baum (1971), Lucas (1979), Clark and Gould (1975), Thomasson (1978a; 1978b, 1980, 1981, 1986), Shaw and Smeins (1979), Terrel and Wergin (1981), Terrel et al. (1983), Webster and Hatch (1983), Barkworth (1983), Peterson (1989), Soderstrom and Zuloaga (1989), Kellogg (1990), Zuloaga and Judziewicz (1991), Valdes-Reyna and Hatch (1991), Molina (1993), Naredo et al. (1993), Ball et al. (1993, 1999) and Snow (1996, 1998).

Caryopsis morphology has received a lot of attention since the beginning of the century; however, most studies have focused on the general morphology and the structure of the embryo. There is comparatively less information available on the anatomy of the caryopsis coat in various other grasses (Netolitzky 1926; Anderson 1927; Avery 1930; Krauss 1933; Hayvard 1938; Akerberg 1943; Bradbury et al. 1956; MacLeod & Palmer 1966; Kowal & Rudnicka-Sternowa 1969; Rost 1973; Jones & Rost 1989; Rost et al. 1990; Ungurean & Costea 1994, 1997). According to our knowledge, micromorphology and anatomy of the caryopsis in *Echinochloa* have not been studied so far.

The purpose of this study is to evaluate the taxonomic usefulness of select floral characters in *Echinochloa*, namely, micro- and macrocharacters of the lemma and caryopsis, the caryopsis coat, and the size of starch grains. Furthermore, the nomenclature, the taxa limits and the interspecific relationships in *Echinochloa* are also discussed.

MATERIAL AND METHODS

Samples were collected and identified from populations in Spain and Romania.

The accessions from Spain were collected and identified by Professor José Luis Carretero from Polytechnic University Valencia, Spain (Table 1). The samples from Romania were collected and identified by the first author (Table 1). Mature spikelets were collected from the median region of the panicles as the spikelets from the upper parts of the inflorescence tend to be smaller. Micromorphological characteristics were assessed on 20 specimens in each population. Voucher specimens for all the taxa are preserved in the VALA, BUAG and BUC Herbaria collections.

Micromorphology of sterile lemmas and caryopses.—Ten mature caryopses for each specimen were examined. Only the adaxial (ventral) face of sterile lemmas and caryopses was observed. Sterile lemmas and caryopses were mounted on aluminium stubs with Avery's spot-o-glue and then coated with 20 nm of gold using Bio-Rad Sputter-Coater SC-500. Samples were examined with 0° tilt at 5–15 KV on a Hitachi S-4100 Scanning Electron Microscope.

Structure of the caryopsis coat.—Mature caryopses with the glumes and bracts removed were soaked in warm water for 1 hour. Afterwards, they were fixed in FAA (90 ml 95% ethanol, 5 ml formalin and 5 ml glacial acetic acid) for 48 h. Caryopses were transferred to 70% ethanol, dehydrated in tertiary butyl alcohol (TBA), and embedded in Tissuemat. Ten mature caryopses for each specimen were serially sectioned to 5–10 µm, stained with safranin and fast green, mounted in Canada balsam, and examined with standard brightfield optics and with polarized light. A small number of caryopses belonging to each accession were soaked, fixed, embedded and sectioned without removing the glumes and bracts. The anatomy drawings were made using a Reichart camera lucida. The lengths of the largest fifty starch grains located in the mealy endosperm from each caryopsis, from each accession were measured as well.

SPIKELETS AND LEMMATAL MICROMORPHOLOGY

Depending on the environmental conditions, an *Echinochloa* spp. plant can produce 1500–22000 spikelets distributed on 9–25 panicle bearing culms. The spikelets have 2 flowers; the lower floret is sterile consisting only of lemma and palea. Sometimes the lower floret is staminate (especially in *E. colona*). The sterile lemma may be awned; but this character is relatively insignificant. The spikelets of *E. colona* are unawned, those of *E. oryzoides* are always awned, and those of the other species may be awned or not. An important character, emphasised by all authors, is the size of the spikelets. The lower glume is about 1/2 the length of the spikelets in *E. colona*; 1/2–3/4 in *E. crus-galli*, *E. oryzoides* and *E. hispidula*, and 1/2–3/5 in *E. oryzicola*. The lemma (in the species examined) is becoming indurated and difficult to remove. Micromorphological characters of the lemma for *Echinochloa* include: short cells (silica cells), long cells, bicellular microhairs, papillae and microhairs. Stomata may occasionally occur in all species. Cork cells were not observed on the *Echinochloa* sterile lemmas. Silica bodies are

TABLE 1. Description of sample populations.

Species	Source	Accessions
<i>Echinochloa colona</i>	Spain (VALA ^a)	c1, c2, c3
	Romania (BUAG ^b , BUC ^c)	c11, c12
<i>Echinochloa crus-galli</i>	Spain (VALA)	cs501, cs606, cs825, cs820
	Romania (BUAG, BUC)	cs21, cs22, cs23
<i>Echinochloa hispidula</i>	Spain (VALA)	h802, h803, h805, h811.
<i>Echinochloa oryzoides</i>	Spain (VALA)	os808, os819, os909
	Romania (BUAG)	os31, os35, os40
<i>Echinochloa oryzicola</i>	Spain (VALA)	oa806, oa909
	Romania (BUAG)	oa64, oa69, oa70, oa71

a–Department of Botany, Polytechnic Institute Valencia, Spain.
b–Department of Botany, University of Agronomical Sciences Bucharest, Romania
c–Botanical Garden, University of Bucharest, Romania.

restricted to the intercostal regions. They can be cross-shaped or dumbbell-shaped. Within each category, 2 types can be further recognised.

- Cross-shaped type (ratio length:width = 1:1).
- C1. Silica bodies with the two endings deeply divided (Fig. 1e).
 - C2. Endings only slightly bilobed (Fig. 2b).

- Dumbbell-shaped type (ratio length:width = 1:2).
- D1. The two endings rounded (Fig. 1 a, f).
 - D2. The two endings emarginated or bilobed (Fig. 1d).

Even if one or two types of silica bodies predominate in one species, one sterile lemma may often contain sporadically the other types as well.

Long cells are easily recognizable by their length and their sinuous margins. Long cells are associated with papillae at their distal ends, especially near the apex of lemmas. Bicellular hairs, 30–60 µm long, are present in all species and belong to the *panicoid type* (Tateoka et al. 1959; Amarasinghe & Watson 1988; Watson & Dallwitz 1992–onwards). All the trichomes observed in *Echinochloa* (bicellular microhairs excepted) are more or less macroscopic. If shorter, they are only an earlier stage in the development of macrohairs. They tend to increase in frequency and length toward the distal parts of the lemmas. The marginal veins usually have the longest hairs. They are somewhat shorter or even missing from the median and lateral veins. Macrohairs are present in the intercostal regions but they are usually shorter compared to those of the marginal veins. In *E. oryzicola*, sterile lemmas often appear glabrous in the intercostal regions. The macrohairs are rigid, pointed and oriented toward the apex of the lemma.

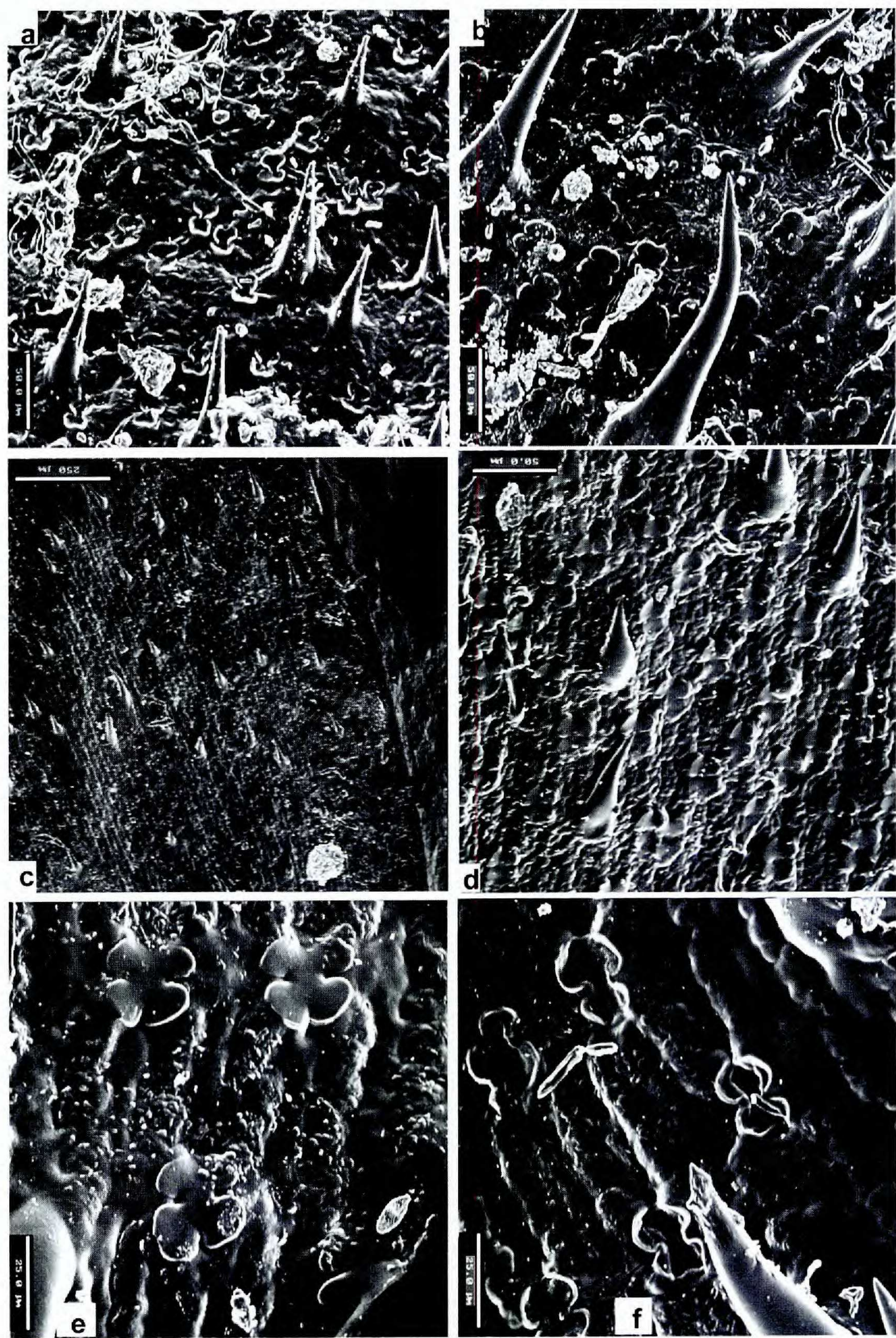


FIG. 1. Micromorphology of lemma. General view. **a.** *Echinochloa oryzoides* (scale bar 50 µm, **b.** *E. hispidula* (scale bar 50 µm), **c–d.** *E. oryzicola* (scale bar 250 µm and 50 µm); silica bodies, **e.** *E. oryzicola* (scale bar 25 µm), **f.** *E. hispidula* (scale bar 25 µm)

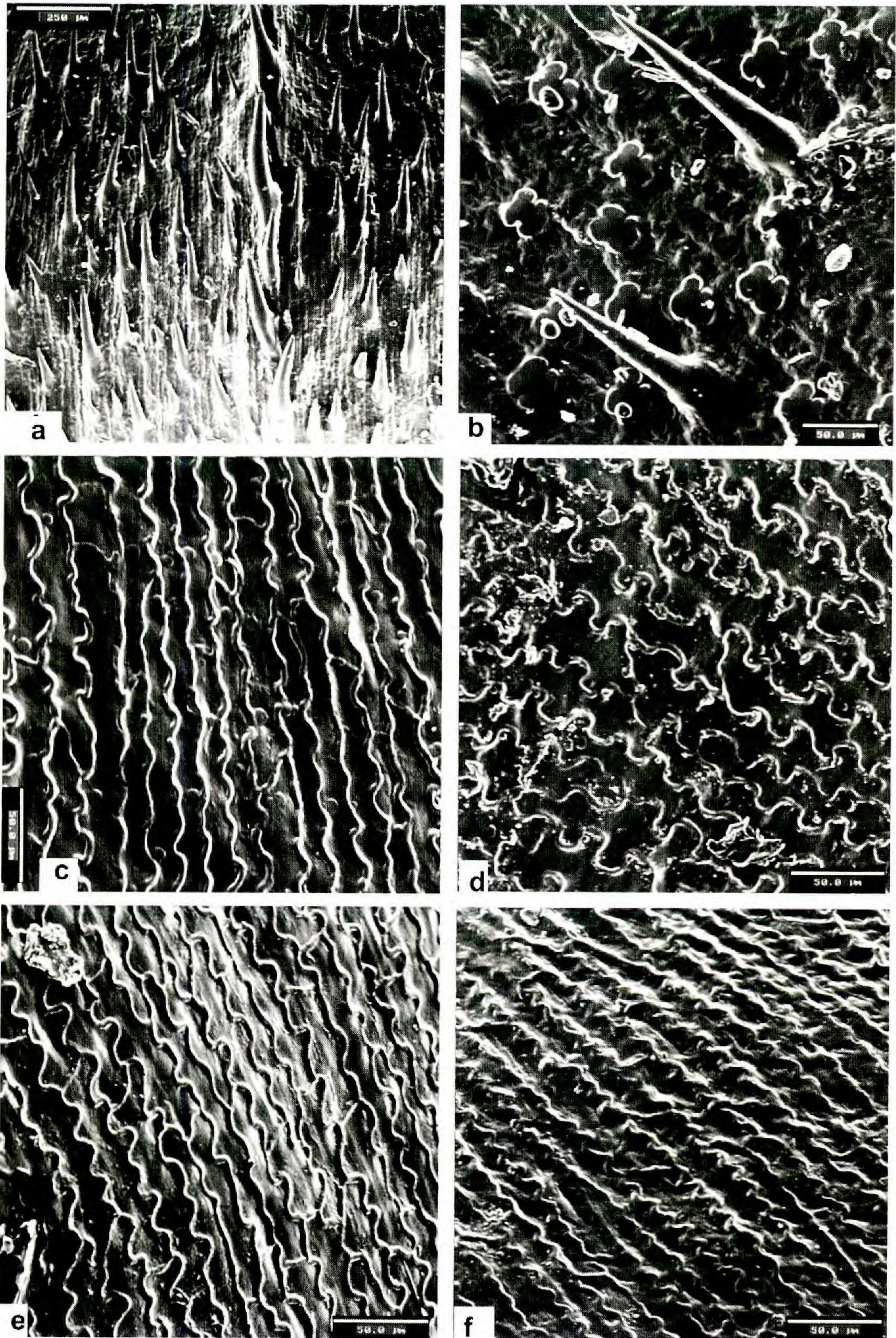


FIG 2. Micromorphology of lemma and caryopsis: **a.** general view of lemma in *Echinochloa crus-galli* (scale bar 250 µm), **b.** silica bodies in *E. crus-galli* (scale bar 50 µm). **c–f** Micromorphology of caryopsis: **c.** *E. oryzoides*, **d.** *E. crus-galli*, **e.** *E. hispidula*, **f.** *E. oryzicola* (scale bar 50 µm).

CARYOPSIS

Morphology of caryopsis (Fig. 3, a-e). Caryopsis is the dry, monospermous, indehiscent fruit of grasses in which the layers of pericarp are fused with the seed coat. The adnation between the pericarp and the seed coat starts in the placentochalazal region and extends toward the rest of the caryopsis (Izaguirre de Artucio & Laguardia 1987).

The size of caryopsis varies proportionally with the size of the spikelet and therefore is also an important differential character. The caryopsis is round, ellipsoid to ovate, with the ventral (adaxial) face rounded and the dorsal face (abaxial) more or less flat. The ventral face shows the axis of the embryo. The embryo is large, about 0.5 times the caryopsis length in *E. colona*; almost as long as the caryopsis in *E. oryzicola* and 0.6–0.7 times the caryopsis length in the other examined species. The scutellar region is visible around the embryo axis. The dorsal face features the basal pointed coleorhiza, which is also encircled by a rounded scutellar region. The hilum may or may not project on the outline of the caryopsis. When plants shed their spikelets, they land with the convex face down, in a position that brings the embryo in the most favourable position for germination. The glumes and sterile lemma then absorb the water necessary for germination. When they land in water, the spikelets float until imbibition is completed after which they sink and fall to the bottom of the water (Costea, unpublished). The mature caryopsis coat is shiny and whitish, yellowish or brown. The scutellar region prolonged around the embryo (on the convex, ventral face), is smooth or wrinkled, and may have black spots (*E. oryzicola*).

Micromorphology of caryopsis (Fig. 2, c-f) is not similar in the *Echinochloa* species examined. The epicarp cells are elongated ranging from 60–120 μm in length and 10–20 μm in width. The periclinal walls are flat, except for *E. oryzicola* which has concave periclinal walls (Fig. 2f). The anticlinal walls are protuberant and undulated with the amplitude, the width at the base and the shape of the undulations having diagnostic value. For example, in *E. crus-galli* (Fig. 2d) the anticlinal walls are Ω -undulated (undulations rounded, wider toward the apex and narrower at the base), in *E. orzyoides* and *E. hispidula* they are S-undulated, (Fig. 2c and e) and in *E. oryzicola* they are Z-undulated (Fig. 2f).

Anatomy of the caryopsis coat (Fig. 4, a-c) in the examined species is similar. The differences observed are minute and quantitative. The caryopsis coat consists of adnate layers of pericarp, seed coat and nucellus that surround the endosperm and embryonic axis. If the lemma is not removed, cross-sections reveal its connivence with the caryopsis. The structure of the lemma resembles the structure of the leaf. A homogenous mesophyll consisting of 2–4 cell layers can be observed between the 2 epidermis. During the early stages of development the mesophyll cells contain chloroplasts. These cells are larger than the epidermis cells, with thickened, sclerified cell walls at maturity (Fig 4, 1-c).

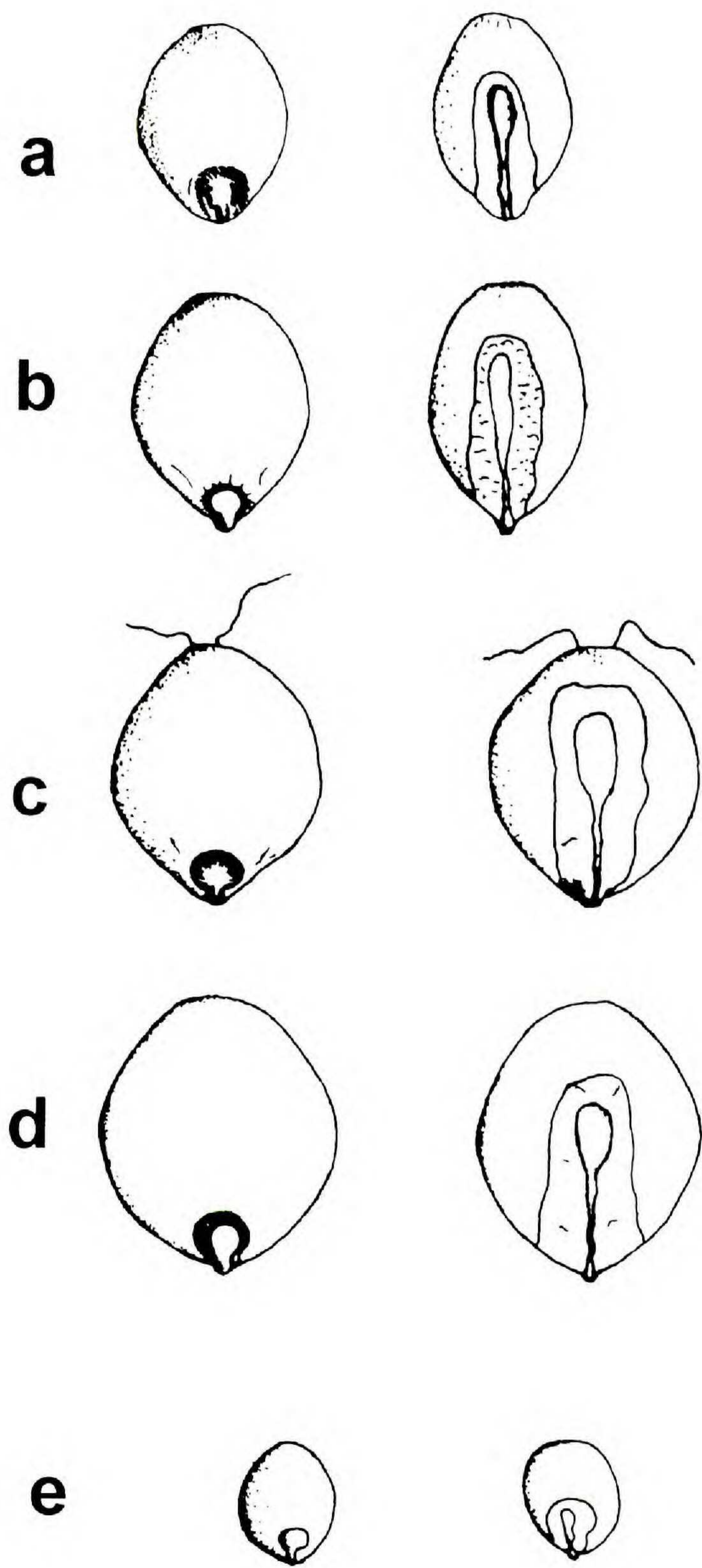


FIG 3. Morphology of caryopsis. **a.** *Echinochloa crus-galli*, **b.** *E. hispidula*, **c.** *E. oryzicola*, **d.** *E. oryzoides*, **e.** *E. colona*. Scale bar 1 mm.

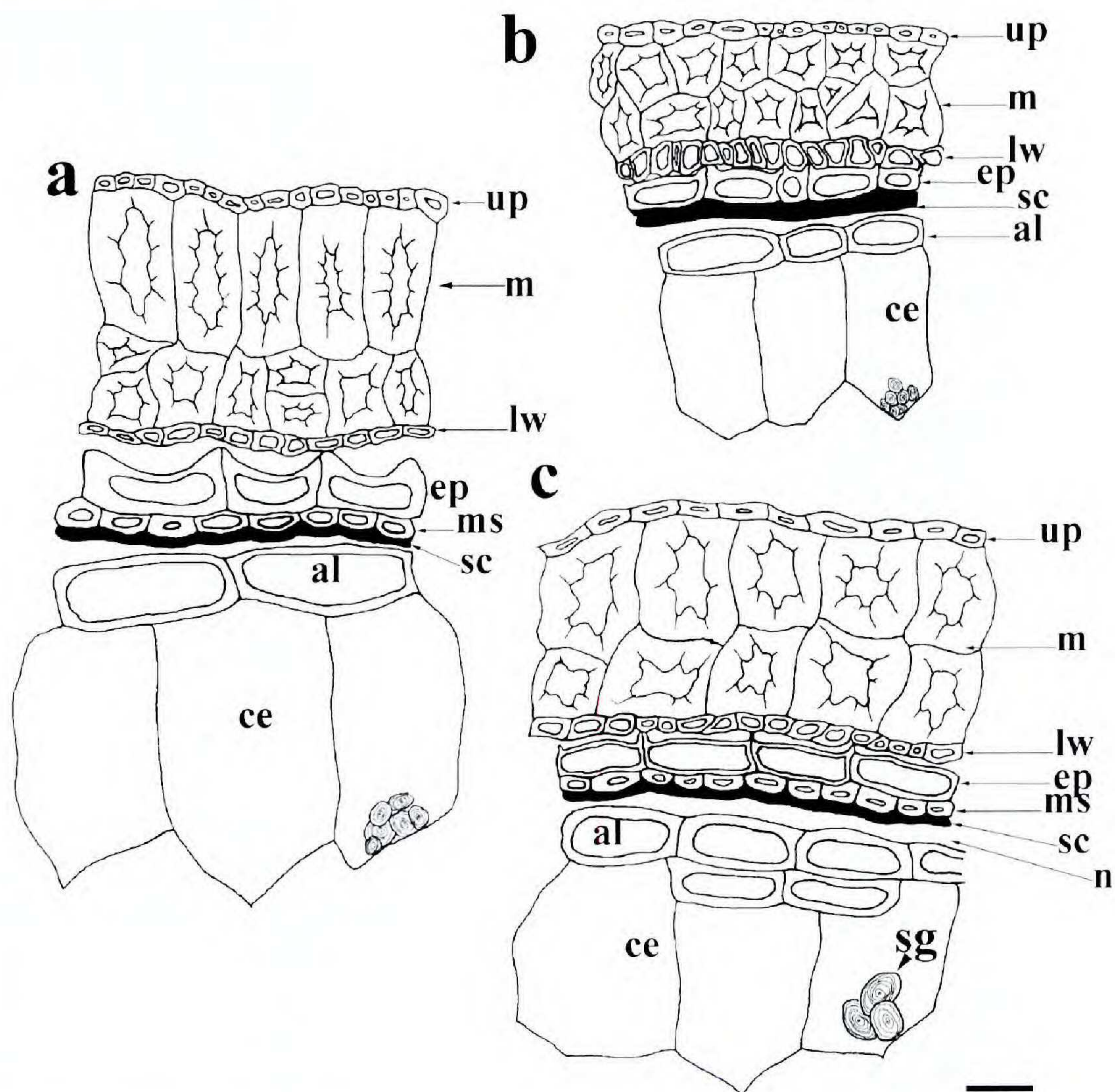


FIG. 4. Anatomy of caryopsis. **a.** *Echinochloa oryzicola*, **b.** *E. crus-galli*, **c.** *E. oryzoides*. **up**—upper epidermis of lemma, **m**—mesophyll of lemma, **lw**—lower epidermis of lemma, **ep**—epicarp, **ms**—mesocarp, **sc**—seed coat, **al**—aleurone layer, **ce**—central endosperm, **sg**—starch grains. Scale bar 10 μ m.

The veins in young lemmas resemble the tertiary veins of the leaves. The caryopsis coat is thin (7–15 μ m thick), with a simple structure. It consists of only 2–3 cell layers. The one-layered epicarp is the most representative component of the pericarp. The epicarp cells have thickened walls. The mesocarp is also single-layered with smaller and often crushed cells. At caryopsis maturity the endocarp is usually no longer visible. In younger caryopses it consists of long thin-walled cells (“tube-cells”), parallel to the epicarp cells. The seed coat is fused with the pericarp and it is not structured, visible only as brown line. The nucellus persists as a thin remnant. A single layered aleurone is continuous around the entire endosperm. The aleurone layer can be locally 2-layered in *E. oryzoides* (Fig. 4c). The central endosperm consists of large, irregularly shaped cells that contain simple starch grains. The central endosperm does not have a homogenous

appearance. Around the embryo the endosperm is “mealy” and soft while in the rest of the caryopsis is hard and glassy. In most of the species examined, the glassy endosperm predominates. However, in *E. oryzoides* the mealy endosperm is equally or better developed than the glassy endosperm. The mealy endosperm contains rounded, isolated starch grains; only rarely they are aggregated (but not compound) in small groups of 2–4 granules. The hard endosperm has polygonal (rarely round) starch grains, closely packed together. This last type corresponds to the *Panicum* type described by Tateoka (1962). The average size of the starch grains is significant and it varies between 5.5 μm and 10.5 μm depending on the species. The embryo has a scutellar tail, without an epiblast.

SPECIES DESCRIPTION AND NOMENCLATURE

Nomenclature.—Most of the nomenclatural problems of *E. oryzicola* are related to the binomial *Panicum phyllopogon* on which *Echinochloa phyllopogon* (Stapf) Stapf ex Koss. is based. Stapf’s diagnosis of *Panicum phyllopogon* addresses only the vegetative features of the plants, particularly the presence of hair tufts in the collar region of the leaves. For a long time this feature was erroneously considered to be an exclusive characteristic of only one species—*E. phyllopogon*, thus generating extensive nomenclatural confusion. The individuals of *Echinochloa oryzicola*—a more recent name—are constantly showing this vegetative characteristic. Consequently *E. oryzicola* has almost generally been considered a synonym of *E. phyllopogon* (Pirola 1965; Morariu 1972; Kerguélen 1975, 1993, 2002; Czerepanov 1981; Michael 1983; Chirilă 1984; Ciocarlan 2000). Kossenko (1940) further contributed to this confusion when he subordinated *E. oryzicola* as a subspecies of *E. phyllopogon* (1940). Other authors erroneously considered *E. oryzicola* to be a synonym of *E. hispidula* (Ohwi 1962; Gould et al. 1972) or even of *E. oryzoides* (Clayton 1980).

Stapf’s collections of *Panicum phyllopogon* at Kew comprise both vegetative and fertile specimens. Tufts of hairs are obvious in most of the vegetative specimens and in several plants bearing inflorescences. Carretero (1981) noted that tufts of hair might also occur in the leaf collar of *E. hispidula* (1981). After examined Stapf’s collection, Carretero (1981) synonymized *E. phyllopogon* with *E. hispidula*. Michael initially regarded Stapf’s collection (1975 in herb, 1983) as a mixture of *E. phyllopogon* (the plants showing the vegetative characteristics) and *E. oryzoides*. Later, after examining populations from Spain, Italy and France he observed that individuals of *E. oryzoides* may also have leaves with hair tufts in the collar region and accordingly he synonymized *E. phyllopogon* with *E. oryzoides*. The author selected as a lectotype for *Panicum phyllopogon* the one sheet in which the inflorescence and tufts of hairs are evident on the same specimen (1985, note in the Kew Herbarium on the specimen selected as a lectotype, collected by Jacometti from “Novarra, in rice fields”). We support

Michael's view in that *E. phyllopogon* may be a synonym of *E. oryzoides* and that Stapf's collection is a mixture of *E. oryzicola* and *E. oryzoides* (= *E. phyllopogon*).

Many recent studies on the biology, ecology, herbicide resistance and physiology have been also using the binomial "*Echinochloa phyllopogon*" referring probably to *E. oryzicola* (Fox & Kennedy 1994; Fox et al. 1995; Mujer et al. 1995; Gibson et al. 1999; Fischer et al. 2000; Fischer et al. 2000).

Identification key.—The following key is modified from Carretero (1981) and Michael (1983).

In order to improve chances of correctly identifying the species, a range of individuals from the same population and a range of spikelets and caryopses belonging to the same plant should be collected and examined. Spikelets length measurements do not include the awns. Caryopsis measurements refer to dry caryopses. Starch grains should be observed in the mealy endosperm (around the embryo).

1. Spikelets 2–3 mm long, regularly arranged on the racemes. Caryopses whitish, 0.7–1.2 mm long with the embryo 0.4–0.5 of the caryopsis length _____ **E. colona**
1. Spikelets larger, irregularly arranged on the racemes. Caryopses larger, light-yellow or in different shades of brown, with the embryo 0.6–0.9 of the caryopsis length _____ **2**
 2. Spikelets 3.9–5 mm long; caryopses 2–3 mm long; starch grains 7–10 μm in diameter _____ **3**
 2. Spikelets 2.8–3.7 mm long; caryopses 1.4–1.8 mm long; starch grains 5–5.6 μm in diameter _____ **4**
3. Coleoptyle red-purplish. Leaves often with a tuft of brown hairs in the collar region. Lower glume 1/2–3/5 the length of the spikelets, with the 3 veins visible only at the base. Sterile lemma often glabrous and shiny, rarely with stiff macrohairs, up to 0.8 mm. Caryopses brownish, 2–2.4 mm long, with the embryo 0.9 of the caryopsis length, and the glassy endosperm equal or more developed than the mealy endosperm _____ **E. oryzicola**
3. Coleoptyle green. Leaves only rarely with a tuft of hairs in the collar region of the leaves. Lower glume 1/2–1/3 the length of the spikelets, with the 3 veins visible along their entire length. Sterile lemma never glabrous and shiny, provided with dense, stiff hairs up to 1 mm long. Caryopsis light-yellow, 2.2–2.8 mm long, with the embryo 0.6–0.7 of the caryopsis length and the mealy endosperm more developed than the glassy endosperm _____ **E. oryzoides**
4. Weeds of rice fields, occasionally with a tuft of hairs in the collar region of the leaves. The panicle is not pyramidal with branches often whorled. Spikelets ovate-elliptical, 3.3–3.8 mm long. Caryopsis 2–2.2 mm long with the scutellar zone transversely wrinkled _____ **E. hispidula**
4. Weeds not obligate of rice, but sometimes occurring in rice fields especially on the margins of the ponds. Leaves never with hairs in the collar of the leaves. Panicle pyramidal with the branches never obviously whorled. Spikelets ovate, 2.8–3.4 mm. Caryopsis ovate, 1.4–1.9 mm, with the scutellar zone smooth _____ **E. crus-galli**

1. *Echinochloa colona* (L.) Link, Hort. Berol. 2:209. 1833. TYPE: "JAMAICA:" Antilles, Browne (LINN). *Panicum colonum* L., Syst. Nat., ed. 10, 2:870. 1759. *Echinochloa crus-galli* (L.) Beauv. subsp. *colona* (L.) Honda, Bot. Mag. (Tokyo), 37:22.1923.

= *Panicum zonale* Guss., Fl. Sic. Prod. 1:62. 1827.

= *Echinochloa verticillata* Berhaut, Bull. Soc.Bot. Fr., 1953:11. 1954.

There is still disagreement over how to write the specific epithet, as various authors have used either “*colonum*” or “*colona*” to designate the species. The specific epithet is most likely derived from the medieval Latin adjective “*colonus-a-um*,” in which case “*Echinochloa colona*” is the correct spelling. Another hypothesis (Carretero 1981) is that the specific epithet results from the contraction of the word “*colonorum*,” the plural genitive of “*colonus-i*,” although we believe this to be less probable.

Echinochloa colona is the most easily recognised species. It is annual, often rooting at the lower nodes. The leaves may have purplish transversal bands. The inflorescence is usually erect, with short branches (the lower ones are shorter to equalling 3 cm long). The spikelets are regularly arranged on the racemes. Often the lower floret of the spikelets is staminate. The lower lemma is awnless, not exceeding 2 mm long. The spikelets are ovate, $2-3 \times 1.2-1.8$ mm. The lower glume is 3-veined, about 1/2 as long as the spikelet. The upper glume is 5-veined. The sterile lemma is 7-veined. The median vein may or may not have macrohairs. Longest macrohairs, 1 mm long. Lateral veins are only distally conspicuous. The silica bodies are of type D2. The stigmas are dark-red.

The caryopsis (Fig. 3e) is round to almost so, whitish and translucent, (0.7–) 0.9–1.2 \times 0.7–1.1 mm. The embryo is 0.4–0.5 of the caryopsis length. The epicarp cells are 40–65 \times 8–12 μ m. The periclinal walls are flat. The anticlinal walls are moderately thick (2.1–2.7 μ m), undulated; the amplitude of the undulations is 5–10 μ m, and their width is 6–12 μ m. The undulations are Ω -shaped or S-shaped. Starch grains, 5.6 (\pm 0.24) μ m long. The chromosome number is $2n = 6x = 54$ (Carretero 1981; Yabuno 1985; Koul & Gohil 1991; Devesa et al. 1991).

This species is a widespread weed in rice fields in tropical and subtropical areas of the globe. In Europe it has been recorded in the warmest countries (Spain, Portugal, Italy, France, Turkey, Greece), where it grows as a ruderal or segetal weed in irrigated crops (and sometimes also in rice). It seems to be expanding towards typical temperate countries where it usually grows as a ruderal. As an example, we are recording the occurrence of this species for the first time in Romania where we have encountered it since 1996 growing as a ruderal in the Railroad Station in Bucharest.

2. *Echinochloa oryzicola* (Vasing.) Vasing. in Komarov, Fl. U.R.S.S. 2:33. 1934. TYPE: “Oriente Extremo inter segetes *Oryzae sativae* L.” *Panicum oryzicola* Vasing., Bull. Appl. Bot. Pl.-Breed. (Leningrad) 25(4):125. 1931. *Echinochloa phyllopogon* (Stapf) Koss. subsp. *oryzicola* (Vasing.) Koss., Not. Syst. Herb. Acad. U.R.S.S. 8(12):210. 1940. *Echinochloa crus-galli* (L.) Beauv. var. *oryzicola* (Vasing.) Ohwi, Acta Phytotax. Geobot. 11:38. 1942.

= *Echinochloa phyllopogon* auct., non Stapf

Annuals; the European populations with a tuft of brownish hairs in the collar

region of the leaves. The hairs are obvious from the two or four leaf stage. Yabuno (1962, 1981) studying Asian populations found that different forms – notably his C and F forms – do not always exhibit the tuft of hairs in the collar region of the leaves. The inflorescence is normally erect and spreading but occasionally can be horizontal or pendent and may be green to red coloured. Spikelets are ovate-elliptical, awned (awn not exceeding 2 cm in length) or not, measuring $3.9\text{--}4.8(-5) \times 2.2\text{--}2.4$ mm. The spikelets persist in the panicle longer than in *E. oryzoides*. The lower glume is about $1/2\text{--}3/5$ the length of the spikelet, with 3 veins only partially visible. The upper glume is 5–7 veined. The sterile lemma is 4–5 veined. The median veins may or may not have short hairs (0.5–0.6 mm); the lateral veins are conspicuous only toward the apex. The longest macrohairs are up to 0.8 mm long. The sterile lemma can be: a) glabrous and shiny, convex – with the lateral veins visible only along their distal part. In the intercostal regions the macrohairs are rare, short, 0.1–0.4 mm, with a swollen base (Fig. 1, c and d) (C-form of Yabuno 1962, 1981). This is the most common type encountered in Europe. b) more or less flat and coarse, with dense long macrohairs, up to 0.8 mm in the intercostal regions (F-form of Yabuno 1962, 1981). The silica bodies may be type C2 (Fig. 1e) or D2 (Fig. 1d). The stigmas are red. The caryopsis is ellipsoidal to almost round measuring $2\text{--}2.4 \times 1.8\text{--}2.1$ mm (Fig. 3c). The embryo is 0.75–0.9 of the caryopsis length. Often the stigmas are persistent. The hilum is prominently visible on the outline of the caryopsis. The colour is brownish-red, brownish-green or brownish-grey. The scutellar zone is irregularly wrinkled often with black spots. The epicarp cells are $100\text{--}120 \times 15$ µm. The periclinal walls are concave (Fig. 4a). The anticlinal walls are moderately thick (2.6–3.2 µm) and undulated; the amplitude of the undulations is 8–10 µm, and their width is 6–7 µm (Fig. 2f). The undulations are Z-shaped (acute and narrow toward the apex) (Fig. 2f). The glassy endosperm predominates or it is as developed as the mealy endosperm. Starch grains are $7.14 (\pm 0.51)$ µm in length. The chromosome number is $2n = 4x = 36$ (Carretero 1981; Yabuno 1985, 1996).

This species originated in China and SE Asia and is now a weed of rice in Europe, Asia, North and South America. The biology and ecology of a cultivated form of *E. oryzicola* has been recently described by Hirose et al. (2000).

3. *Echinochloa crus-galli* (L.) Beauv., Ess. Agrost.:53, 161, tab. 11, fig. 2. 1812. TYPE: “Europae, Virginiae cultis” (LINN). *Panicum crus-galli* L., Sp. Pl., ed. 1:56. 1753. *Milium crus-galli* (L.) Moench, Meth:202. 1794.

The herbarium sheet number 80.18 (LINN) contains a specimen collected by Kalm in Canada, annotated by Linnaeus himself as *Panicum crus-galli*. Several authors (Hitchcock 1920; Baum 1967; Carretero 1981; Michael 1983) observed that this specimen does not belong to *E. crus-galli*. The same situation occurs with the other two sheets labelled *Panicum crus-galli* (80.19 and 80.20) by Linnaeus. According to Carretero, only the specimen 80.17 labelled by Linnaeus as *Panicum crus-corvis* corresponds to *E. crus-galli*. Ali (1968) and Gould et al. (1972) designated a neotype. Michael (1983) designated as a lectotype the specimen 1: 303

from Burser's Herbarium at the University of Uppsala [in order to retain the specific epithet, Baum suggested the same solution but he did not select a lectotype (1967)].

= *Panicum crus-corvi* L., Sp. Pl., ed. 2, 1:84. 1762.

Annuals with erect to spreading or decumbent stems, up to 120 cm. The panicle is often pyramidal with purplish nuances, erect, but sometimes nodding. The inflorescence branches are longer than 3 cm, patent or erect-patent, never obviously whorled. The lower branches are frequently twice branched. The spikelets are irregularly arranged on the racemes and the lower floret is rarely staminate. Spikelets are ovate to broadly-ovate, $2.8\text{--}3.4 \times 1.6\text{--}1.8$ mm. The lemma of the lower floret is awnless or awned, the awn not exceeding 5 cm in length. The lower glume is 3-veined and about $1/2\text{--}1/3$ the length of the spikelet. The upper glume is 5-7 veined. The sterile lemma is 7-veined. The lateral veins are visible along their entire length or only toward the apex. The longest macrohairs are about 1 mm long. The silica bodies belong to types C2 or D2 (Fig. 2b). The stigmas are white or red.

The caryopsis is ovate, $1.4\text{--}1.9 \times 1.3\text{--}1.6$ mm, brownish-red or brownish-grey in colour. The embryo is 0.6-0.7 of the caryopsis length (Fig. 3a). The epicarp cells are $60\text{--}80 \times 10\text{--}15$ μm . The periclinal walls are flat. The anticlinal walls are thick ($2.6\text{--}3.2$ μm) and undulated; the amplitude of the undulations is 8-10 μm , and their width is 6-7 μm . The undulations are Ω -shaped (Fig. 2d). The glassy endosperm predominates. The starch grains are 5.9 μm (± 0.37) in length. The chromosome number is $2n = 6x = 54$ (Carretero 1981).

This species is probably the most widespread of the genus, being a common and noxious weed all over the world, especially in irrigated crops. It is less limited to warm climate compared to *E. colona* and *E. hispidula*. In rice it usually grows on the pond margins, but it may also penetrate the interior of the rice fields.

4. **Echinochloa hispidula** (Retz.) Nees ex Royle, Ill. Bot. Himal. 11:416, 420. 1840.

TYPE: "India Orientali," König (LD). *Panicum hispidulum* Retz., Obs. Bot. 5:18. 1789. *Echinochloa crus-galli* (L.) Beauv. var. *hispidula* (Retz.) Honda, Bot. Mag. (Tokyo) 37:122. 1923. *Echinochloa crus-galli* (L.) Beauv. subsp. *hispidula* (Retz.) Honda, J. Fac. Sci. Tokio Univ., Bot. 3:267. 1930.

= *Echinochloa phylloryzoides* Novelli, Giorn. Risc. 2:306 (1912).

= *Echinochloa erecta* (Pollacci) Pignatti, Arch. Bot. (Italy) 31, ser. III, 15(1):2. 1955. *Echinochloa crus-galli* (L.) Beauv subsp. *erecta* (Pollaci) Ciferri & Giacomini Nomencl. Fl. Ital. 1:20. 1950.

Annuals which may occasionally have tufts of hairs in the collar region of the leaves. The panicle is rarely pyramidal, erect to pendent, green or with purplish nuances. The branches are whorled and more or less erect, except for the lowermost ones. Spikelets are ovate-elliptical of $3.3\text{--}3.6(-3.8) \times 1.7\text{--}1.8(-2)$ mm. The lower glume is 3-veined, about $1/2\text{--}1/3$ of the spikelet length, and the upper glume is 5-7 veined. The sterile lemma is 7-veined resembling *E. crus-galli*. The longest macrohairs are about 0.8 mm long (Fig. 1b). The silica bodies are very

variable, depending on the population – C1 (h802) (Fig. 1b), C1 and D1 (h803, h805), C2 and D2 (h805). The stigmas are white but may occasionally be red.

The caryopsis is larger than that of *E. crus-galli*, ovoid to oblong, $2\text{--}2.2 \times 1.5\text{--}1.8$ mm and brownish-red or brownish-grey in colour (Fig. 3b). The embryo is 0.6–0.7 the caryopsis length, and the scutellar zone is transversally wrinkled (Fig. 3b). The hilum is projecting on the outline of the caryopsis. The epicarp cells are $65\text{--}90 \times 10\text{--}15 \mu\text{m}$. The periclinal walls are flat. The anticlinal walls are thick ($2.6\text{--}3.2 \mu\text{m}$) and S-undulated; the amplitude of the undulations is $8\text{--}10 \mu\text{m}$ and their width is $6\text{--}6.5 \mu\text{m}$ (Fig. 2e). The glassy endosperm predominates. The starch grains are in average $6.3 (\pm 0.47) \mu\text{m}$ in length. The chromosome numbers reported are: $2n = 6x = 54$ (Devesa et al. 1991) or $2n = 36$ (Carretero 1981; Feng & Zhang 1993).

This taxon probably originated in the SE Asia. It is widespread in tropical and temperate areas of Asia, Africa, America and Australia. In Europe it grows only in the warmest regions (Spain, Italy, Portugal and France) as a weed of rice fields.

5. *Echinochloa oryzoides* (Arduino) Fritsch, Verh. Zool.-Bot. Ges. Wien 41: 742. 1891. TYPE: “Semina hujus Panici inventa a me fuere inter Oryzam” *Panicum oryzoides* Arduino, Animadv. Bot. Spec. Alt. 16, tab. 5. 1764. *Panicum crus-galli* L. var. *oryzoides* (Arduino) Fiori, Nuov. Fl. Anal. Ital. 1:79. 1923.

- = *Echinochloa crus-galli* (L.) Beauv. subsp. *oryzoides* Bolos & Masclans, Collect. Bot. 4:420. 1955.
- = *Panicum hostii* Bieb., Fl. Taur. Cauc. 3:57. 1819. *Echinochloa crus-galli* (L.) Beauv. subsp. *hostii* (M. Bieb.) K. Richter, Pl. Eur. 1:26. 1890.
- = *Panicum phyllopogon* Stapf, Hook, Ic. Plant., ser. 4, plate 2698. 1901. *Echinochloa phyllopogon* (Stapf) Stapf, ex Koss., Not. Syst. Herb. Acad. U.R.S.S. 8 (12):208. 1940.
- = *Echinochloa macrocarpa* Vasing. in Komarov, Fl. U.R.S.S. 2:739. 1934. *Echinochloa crus-galli* L. Beauv. var. *macrocarpa* (Vasing.) Morariu in Savulescu, Fl. Rom. 12:86. 1972.
- = *Echinochloa coarctata* Koss., Not. Syst. Herb. Acad. U.R.S.S. 9(1):28. 1941.
- = *Echinochloa commutata* Schultes in Roemer & Schultes, Syst. Veg., ed. 15, Mant. 2:267. 1824.

Annuals with erect to spreading or decumbent stems, up to 130 cm tall. The seedlings have a reddish coleoptyle. Tufts of hairs in the collar region may be infrequently present. The inflorescence is green, pendent and at maturity hanging almost horizontally, resembling rice in habit. The branches of the panicle are often adpressed to the main rachis. The spikelets are rather persistent, usually awned (awn up to 5 cm long), broadly-ovate to ovate and $(3.6\text{--})4.1\text{--}5 \times 2.2\text{--}2.6 \mu\text{m}$. The lower glume is about 1/2–1/3 the length of the spikelet, with 3 veins visible across their entire length. The upper glume has 5 veins also entirely visible. The sterile lemma is 7-veined, with the lateral veins usually visible along their entire course. The longest macrohairs are about 1 mm long (Fig. 1a). The silica bodies belong to the type D1 (Fig. 1a). The stigmas are red.

The caryopsis is ovate to almost round, $2.2\text{--}2.8 \times 1.9\text{--}2.3$ mm (Fig. 3d) and yellowish. The embryo is 0.6–0.7 the caryopsis length, with the scutellar region

zone smooth (Fig. 3d). The epicarp cells are $100\text{--}120 \times 10\text{--}15\ \mu\text{m}$. The periclinal walls are flat. The anticlinal walls are moderately thick ($2\text{--}2.6\ \mu\text{m}$) and weakly S-undulated (Fig. 2c). The amplitude of the undulations is $1\text{--}3\ \mu\text{m}$, and their width is $8\text{--}11\ \mu\text{m}$. The mealy endosperm predominates. The starch grains are $9.5\ \mu\text{m}$ (± 0.58) in length. The chromosome numbers reported are: $2n = 36$ (Carretero 1981) and $2n = 6x = 54$ (Yabuno 1984; Feng & Zhang 1993).

The species is a common weed in rice occurring in many countries from Asia, Europe, North America, South America and Australia. It is probably one of the most widespread species after *E. crus-galli* and *E. colona*.

DISCUSSION

Characters

The genus *Echinochloa* does not have qualitative characters which clearly demarcate its species. A good example is the presence of hair tufts in the collar region of the leaves which has been considered an exclusive feature of *E. phyllopogon*. This assumption has subsequently caused a widespread nomenclatural and taxonomic confusion because as we have previously indicated, three species may show this feature (*E. oryzicola* commonly; *E. hispidula* and *E. oryzoides* rarely). Even the most significant qualitative character states overlap between species. When such characters are noted they are always accompanied by the words “often,” “usually,” “normally,” etc. because exceptions are possible. The occurrence of a feature should be understood as a predilection and not as an exclusive characteristic.

Lemmatal micromorphology.—The long cells, microhairs and papillae are the same in all species examined. The pattern of papillae in *Echinochloa* species is similar to the pattern described in the fertile lemmas of some *Panicum* species (Clark & Gould 1975). The macrohairs are more or less similar in the examined taxa. Shorter hairs that could be described as prickles (Metcalf 1960; Ellis 1979) were observed in all species. However, because these shorter hairs represent a developmental stage, only the macrohairs are recognised in this study as a distinct category (see Snow 1996, 1998 for considerations on homology and ontogeny of hairs in *Poaceae*). Variations in length, distribution and density of macrohairs are minute and there is considerable overlapping among species. The only exception is the short, rare macrohairs, with swollen bases from the intercostal regions of sterile lemmas in *E. oryzicola* (in the “form C” of Yabuno 1962, 1981). These hairs are constant in their morphology and can be considered intermediate to prickles (Metcalf 1960; Ellis 1979). Silica bodies have previously been considered structures of taxonomic significance in *Poaceae* (Metcalf 1960; Ellis 1979; Palmer & Tucker 1981; Evoli & Pirola 1971). In *Echinochloa*, silica bodies vary in shape even within a small area of the same lemma. However, in most species there is a tendency toward one or two types. *Echinochloa hispidula* was the most variable of all species examined in this

study. The silica bodies varied from population to population, with all the different types observed. The previous epidermis studies conducted on leaves (Sanchez 1968; Pirola & Evoli 1971; Carretero 1981; Jin et al. 1986) are rather contradictory but they all showed an even greater variation of this character. Even if the results obtained in this study revealed some differences between species (*E. hispidula* excepted), the shape characteristics of the silica bodies should be regarded with caution. More populations need to be examined before a final conclusion is reached. The same cautionary approach towards the taxonomic utility of the silica body shape is suggested by other studies conducted on *Zizania* (Terrell & Wergin 1981), *Oryza* (Whang & Kim 1994) and *Leptochloa* (Snow 1996). Ball et al. (1999) showed that silica phytoliths examined individually are taxonomically irrelevant. The authors instead used detailed morphometrics, computer-assisted imagery and statistical analysis to develop a classification key of several *Triticum* and *Hordeum* species. The presence or absence of silica bodies in lemmas can prove useful at higher ranks (genera and above) since their presence is probably symplesiomorphic (Snow 1996).

Caryopsis.—The simple morphology of the caryopsis provides good characters for species identification. The size of caryopsis is important and correlated with the size of the spikelets. The other characters overlap between species but may be useful diagnostics in some cases, eg: caryopsis whitish, translucent (*E. colona*), yellowish (*E. oryzoides*); embryo 0.4–0.5 of the caryopsis length (*E. colona*) or 0.75–0.9 (*E. oryzicola*). Surprisingly, surface patterns of the caryopsis proved to be significant in the differentiation between almost all *Echinochloa* species. However, more populations should be examined before any definite conclusions can be reached.

The anatomy of the caryopsis is of minimal systematic value. The overall organization of the caryopsis coat resembles the structures described in *Setaria* (Rost 1973) or *Melica* (Rost and Izaguirre de Artucio 1990). The structural simplicity of the pericarp can be a functional result of the indurated lemma that protects the caryopsis. In those grasses where no coalescence between the caryopsis and lemma occurs, or when the lemma is thin, the pericarp is more complex structurally (as for example in many *Triticoideae*—Netolitzky 1926; Avery 1930; Krauss 1930; Bradbury et al. 1956; Ungurean & Costea 1994). The anatomy of the sterile lemmas in *Echinochloa* species could be more important as a taxonomic character than the structure of the caryopsis coat. The structural features and surface pattern of the lemma indicate its ontogenetic connection with the leaves.

The average size of the starch grains examined in a large number of endosperm cells and caryopses is constant and significant among the species examined and therefore can be considered a diagnostic feature. This character is as significant in the taxonomy of the genus as other quantitatively important characters such as the size of spikelets, and size of caryopses.

Relationships between species

The individuality of *Echinochloa* species as treated in the present study is apparently reinforced by studies of their biology and ecology (Holm et al. 1977, 1997; Szilvássy 1976; Chirilă 1967; Carretero 1981; Yabuno 1983; Norris 1996; Honek & Martinova 1996). The appropriate understanding of *E. oryzicola* was delayed by nomenclature problems since this binomial has been almost generally considered a synonym of *E. phyllopogon* (Pirola 1965; Morariu 1972; Kerguélen 1975, 1993, 2002; Czerepanov 1981; Michael 1983; Chirilă 1984; Ciocarlan 2000). Apart from this nomenclatural confusion *E. oryzicola* is the second species easiest to differentiate (after *E. colona*) even using classic morphologic characters. It has the second largest (after *E. oryzoides*) spikelets, caryopses and starch grains; the micromorphology of the sterile lemma and caryopsis are quite peculiar as well.

Yet apart from *E. colona* and *E. oryzicola*, which are usually easily recognisable, the other 3 taxa comprise a difficult complex. *Echinochloa hispidula* is extremely variable and shares close affinities with both *E. oryzoides* and *E. crus-galli*. Several current treatments tend to view *E. hispidula* as a subspecies or as a variety of *E. crus-galli* (Michael 1983; Mateo Sanz 1990; Devesa 1991; Janzein 1993; Mateo Sanz & Crespo Villalba 1995; Kerguélen 1993, 2002; Asíns et al. 1999). However, Gonzales-Andres et al. (1996) studying the isoenzyme variation of these species, reached another conclusion: only 3 species—*E. colona*, *E. crus-galli* and *E. oryzicola*—were clearly defined. *Echinochloa hispidula* and *E. oryzoides* clustered together, and the variability between the populations of *E. hispidula* was higher than the variability between both taxa. Therefore, the authors suggested that the most appropriate classification would be *E. hispidula* as a subspecies of *E. oryzoides*. Asíns et al. (1999) studying the morphologic and isozyme patterns of variation of the same species, found only *E. colona* and *E. oryzicola* to be distinct from both morphologic and molecular point of view. Based on their morphology, the populations of *E. crus-galli*, *E. hispidula* and *E. oryzoides* congruently clustered together within each species. However, based on the isozyme variation, there was a considerable overlapping between species suggesting a high degree of genetic variation. Consequently, Asíns et al. (1999) advocated that *E. hispidula* and *E. oryzoides* as infraspecific taxa of *E. crus-galli* would be the most appropriate classification. We consider that in order to reach a final conclusion more populations worldwide should be analysed using combined molecular (such as RAPD, AFLP, ISSR and DNA fingerprints) and morphologic methods, and the data resolved in a cladistic approach involving all characters. The enormous variation observed makes the boundaries between these taxa rather uncertain and in order to avoid an arbitrary classification, we maintained each taxa at specific level. In *Echinochloa* the amplitude of morphologic variation can serve as a basis for taxa differen-

tiation. Each taxon has a distinct morphologic core and the variation—statistically understood—can serve to their delimitation.

ACKNOWLEDGMENTS

I owe many thanks to Jose Luis Carretero for the useful discussions and the material from Spain. I am also very grateful to Julio Iranzo who kindly made possible the SEM study. Our sincere thanks go also to Peter Michael and W.D. Clayton who reviewed an earlier version of the manuscript providing valuable comments and suggestions. Many thanks go also to Cheryl Corbett for the helpful criticism.

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